IV. MORPHOLOGICAL FEATURES OF CERTAIN MUSSEL-SHELLS FOUND IN LAKE ERIE, COMPARED WITH THOSE OF THE CORRESPONDING SPECIES FOUND IN THE DRAINAGE OF THE UPPER OHIO.*

By Norman McDowell Grier.

(PLATES II-III.)

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usual scientific zeal most unselfishly contributed such of his own observations as seemed to have a direct bearing upon the matter in hand. Too much can not be said in appreciation of the kindness of Dr. Ortmann, while almost equal indebtedness is felt toward Dr. O. E. Jennings of the Museum.

From time to time I called upon other eminent and enthusiastic students of the *Naiades* for the benefit of their experiences in certain phases of the problem. Those who have cheerfully responded are Dr. Bryant Walker, Dr. C. B. Davenport, Dr. A. F. Shira, Director of the Biological Station at Fairport, Iowa, and Messrs. W. I. Utterback, Calvin Goodrich, and L. S. Frierson. Finally my thanks are due to Miss D. M. Smith, a Y. M. C. A. Welfare Worker in France, who aided considerably in the revision of the text.

II. INTRODUCTORY.

The primary purpose of the investigation here recorded has been to determine as precisely as possible in morphological terms what are the distinctions which exist between the species of *Naiades* found in the upper drainage of the Ohio River and their varieties in Lake Erie; and secondarily by a comparative examination of these differences to endeavor to reach definite conclusions as to the effects produced by the two environments as causative of these differences.

As with other classes of Mollusca, if we except such work as that of C. C. Adams $(I)^*$ on the freshwater snail *Io*, the phases of local variation in American species have received rather indifferent treatment from zoölogists. While they have been made the subject of comment in a number of scattered papers by European investigators dealing with American forms, they have principally received attention in the more purely economic publications of the U. S. Bureau of Fisheries, and there, as the examination of the literature shows, only incidentally from an ecological rather than from a morphological standpoint.

L. V. Hueber (20) writing upon *Unio fasciculus* records physical differences between individuals of this species found in rivers and canals. He notes that the growth-lines are more distinct in the quieter waters of canals; that, when viewed from in front, mussels from the rivers appear wedge-shaped, those from the canals more oval. Julius

* The numbers in parentheses refer to the Bibliography, Section XI of this paper.

Hazey (16) deals with Unio pictorum. He states that in rapidly flowing brooks the shells become long, straight, narrow, with narrow growth-lines and rounded extremities, while in the quiet waters of the main stream (Danube) is found a high, flat form, with broad lines of growth, rounded posteriorly, and with short anterior border. He further remarks that transitional forms representing this species occur in places intermediate between the swift brooks and the quieter river, and points out that typical Unio pictorum is developed in stagnant water, but in swifter currents becomes elongate, producing the variety longirostris. He shows that the "beak" obtains its greatest growth in swiftly flowing streams. An excellent paper by H. Wallengren (56) deals at some length with the matters which the two previously mentioned writers discuss.

With the appearance of the paper of H. Sell (45) there began a revival of interest in this particular field of investigation, which has continued to the present time. As the result of extensive comparisons Sell concludes that in mussels found in certain lakes and rivers the anterior portion of the shell is thicker in the latter and weaker in the lakes. He associates a long rather than a curved lower border with strong currents, regarding it as giving greater protection. Lake forms are comparatively inflated and have protruding growth-rings. He accounts for the presence or absence of the growth-rings by the degree of the disturbance of the water. Forms from still water are somewhat more symmetrical in outline, and he states as a general principle that the size of *Unios* seems to be proportionate to the size of the body of water in which they are found.

O. Buchner (5) observes that Anodouta sp. reaches its greatest development on muddy bottoms, becoming compressed in brooks. This alteration in the shape of the shells, resulting in the production of varieties, he is inclined to attribute to nutritive conditions. He also recognizes transitional forms originating in the different environments. W. V. Israel (22, 23, 24) besides corroborating the statements made by the writers already quoted, dwells at length upon Unio crassus, noting that it is shorter in brooks than in quiet waters (cf. V. Hueber) in which it becomes larger, with a curved inferior border. In strong streams and cataracts, especially where gravel is found, he observes that the mussels become stronger in structure, shortened, and rounded. He distinguishes three varieties of Unio pictorum formed in the way indicated: (a) the common typical form of the larger rivers; (b) a form as broad or broader than long from sandy bottoms; (c) a thickshelled form from rapid waters. He adds that forms from still water and muddy streams have a prolonged posterior end, which is not so well developed in rapid currents.

M. C. March (30) apparently began a statistical study along the same lines pursued in this paper, plotting variation curves based upon the relation between the antero-posterior or horizontal axis and the dorso-ventral or perpendicular axis. Only a short note was published, of which the following summary is given. March states that in Unio tumidus and Unio pictorum two main types of shell occur: one stout and heavy with relatively long dorso-ventral axis; the other with short antero-posterior axis, etc. March believes that the growth of the anterior portion of the shell is slower than that of the posterior portion, "as is natural with an animal, which has to plough its way through the mud." An increase in the rate of the current in which they live would produce a decrease in pre-umbonal development, and thus tend to give the umbo a more forward position in those forms which inhabit strong currents. Such forms are found in canals having strong gradients, those otherwise modified in deeper canals with an abundance of locks. Thick mud is supposed to induce elongation, slow rivers develop forms with long dorso-ventral axes.

A paper by Clessin (6) published later contains many interesting side-lights upon the history of the *Naiades*, but nothing of immediate interest to us. Finally Haas & Schwarz (15) propose as a law the statement, which this paper endeavors as the result of investigation to prove, that "The *same* types under the same biological (ecological) conditions produce the same variants; *different* types under like conditions produce convergent (parallel) local variants. In the case of a sufficiently lengthy isolation the local variants subject to biologically similar environments, may become constant or fixed local forms." (*Free translation*.)

The above completes a resumé of all the European literature to which I have had access. While a large part of it, as well as the literature hereafter cited, may not appear to have much bearing upon the results of the following investigation, I believe that a reference to it is essential to a complete understanding of the nature of the problem. The following references to investigations made upon our American forms are added as bearing upon the same or closely related species, with which I deal later.

Wilson & Clark (59) state that Anodonta grandis is lacustrine by choice, and that in lakes the shell is typically inflated and thinner, while in creeks it becomes it becomes thicker, more compressed, elongated. Later (61) they note that where two closely related forms of Naiades differ essentially in the degree of inflation of the shell, the flatter and less inflated form is found in the upper portions of the river and in its tributaries, while the rounder and more inflated form is confined to the lower stretches of the main stream where there is a weaker current and more mud. They found, however, a notable exception in the case of Symphynota (Lasmigona) costata. They also note that the swiftness of the current, the size of the stream, and the kind of bottom affect other characters of the shell besides its degree of inflation. Further (60) they say: "Below the Cumberland Falls in limestone formations the water contains a considerable percentage of lime. Here the shells are much larger and thicker than above the Falls." Danglade (11) writing with regard to the Illinois River, states that the mussels become smaller in the lower stretches of the stream. He states with regard to Quadrula metanevra that one of the examples before him has 'the markedly pinched posterior dorsal portion' generally found in the lower Wabash. He says of Quadrula *undulata* that it 'becomes inflated lower down the river.' With regard to Obliquaria reflexa he says: "In the Peoria lake-region, where the current is slow and the bottom is composed of soft mud, the shell is often very heavy and rounded anteriorly, while posteriorly it is thin and much elongated, which is no doubt the result of accomodations to natural conditions. In lower stretches the shell, although heavy and inflated, is considerably smaller than those in the upper portions of the river." Of Plagiola elegans he remarks: "Some examples from portions of the river having soft and mud bottoms are greatly elongated posteriorly." Utterback (51, 52) notes that in the Osage River 'flat or compressed forms are found at the head-waters where the water is shallower or swifter, and that they become heavier and more swollen further down stream, where the water is deeper and more sluggish.' He also found that the quiet, sluggish streams of northern Missouri tend to produce a heavy, rarely plicated, highly inflated shell (Amblema); on the other hand the swift clear water of the streams of southern Missouri give origin to compressed multiplicated shells.

Objection to the statement that *Naiades* become more inflated in the lower reaches of streams is offered by that eminent student of the Mollusca, Dr. Bryant Walker (1914–1916) and his view is interesting for the reason that it brings out points which will be later discussed in this paper. In a letter to the writer Dr. Walker mentions two contradictory cases, saying: "Practically all the *Naiades* of the Great Lakes are much smaller than the examples of the same species from the inland streams tributary to the lakes. This may be the result of the great difference in temperature or less abundant food-supply (this also possibly the result of temperature) or the combined result of both." But, as indicated, this may be due to an absolutely different environment, with other unexplainable factors. Again Dr. Walker says: "In the case of *Quadrula elliotti*, which comes from a small creek in N.W. Georgia, where it grows very large, the species seems to run into *Quadrula atrocostata* of the Coosa, which never grows as large as typical *elliotti*."

Ortmann (33, 34, 36, 38, 39) noted that the diameter of certain shells increases in a down-stream direction. Two distinct forms representing what was formerly considered a single species may appear. Thus we have Obovaria subrotunda circulus and Obovaria subrotunda lens; Pleurobema obliquum and Pleurobema coccineum; Fusconaia barnesiana and vars. bigbyensis and tumescens.

Aside from the fragmentary indirect evidence and excepting the work begun by Miss March and the more general observations of Walker presently to be discussed, there appears to have been no systematic study of these peculiar problems, which arise in connection with the development of the Naiades. The rich collection of the Carnegie Museum has afforded excellent opportunity for investigating the matters spoken of and at the suggestion of Dr. Arnold E. Ortmann the writer has undertaken to throw what light he can upon the subject with the help of the abundant material which has been placed at his disposition for study. This material includes the very extensive collections made by Dr. Ortmann in the rivers of western Pennsylvania and in Lake Erie during the years 1903 to 1907 inclusive, together with exchanges representing the fauna of outlying territories. The species employed by me are those which are most abundantly represented in the Museum. I have followed the arrangement and the nomenclature suggested by Sterki (50) and elaborated by Ortmann (33, 35, 36). Priority is accorded in this scheme to many of the names applied by Rafinesque (40) which have been revived by Frierson (13) and Vanatta (53) and accepted by Ortmann. The list of species used by me is here given.

III. LIST OF SPECIES EMPLOYED IN THIS INVESTIGATION (43).

UPPER OHIO.				
Fusconaja flava (Rafinesque).				
Amblema costata (Rafinesque).				
Pleurobema obliquum coccineum				
(Conrad).				
Elliptio dilatatus (Rafinesque).				
Symphynota costata (Rafinesque).				
Anodonta grandis (Say).				
Paraptera fragilis (Rafinesque).				
Proptera alata (Say).				
Anodontoides ferussacianus (Lea).				
Eurynia recta latissima (Rafinesque).				
Lampsilis luteola (Lamarck).				
Lampsilis ovata ventricosa (Lamarck).				

IV. PHYSICAL CONDITIONS AND TYPES OF NAIAD FAUNE.

The physical conditions under which the species enumerated in the foregoing list occur may now be discussed. Lake Erie (Cf. Plates I and II, maps) one of the smaller Great (Laurentian) Lakes has a water surface of 9,960 square miles (42). In the part we are most largely concerned with the immediate shore consists of the soft blue Devonian shale named by Newberry (32) the "Erie shale" covered with a varying thickness of drift clay. A large amount of beach debris is annually taken into the water of Lake Erie from this region and almost the entire shore from Sandusky Bay eastward represents a typical beach of sand or gravel, strewn here and there with boulders from the drift-clay above. Especially after storms the streams flowing into the lake are frequently turbid and heavy with sediment, but the St. Lawrence River flowing from the Great Lakes is usually clear and free from all but the finest material in suspension (25). The coarse sediment brought into the lake is swept along the coast by the shore-currents and mingled with the pebbles and sand derived from the wear of the land by shore-waves, or deposited in stratified layers on the lake-bottom. The finer products of the wash of the land or of shore-erosion are thus carried lakeward. In general, the sheet of material thus spread out is thickest and coarsest near the shore, and becomes finer and thinner as the distance from shore increases. The coarse strata in the shore-deposits overlap and dovetail lakeward with the outer layers of fine sediment in the central part of the basin. So far as the bottom is concerned, conditions in Presque Isle Bay (44), the principal source of material used in this investigation, represent the extreme of finest sediment.

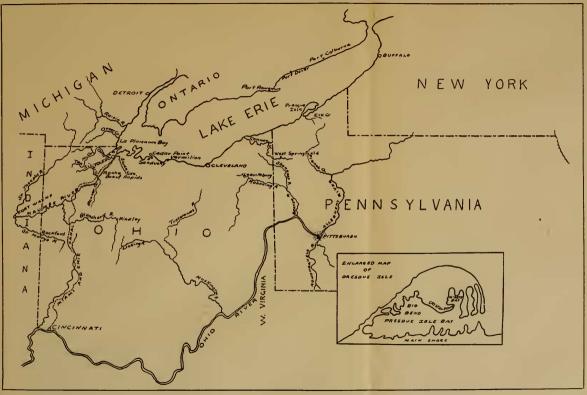
The friction of wind on the surface of the lake produces very decided movements in the waters. On the Laurentian Lakes, waves fifteen to eighteen feet in amplitude have been observed during long, continued storms. As Lake Erie is the shallowest of the Great Lakes and as its axis lies almost directly in the normal path of the cyclonic storms (25), the wave action thus produced is particularly strong at times. The effect of the prevailing westerly winds on the surface movement of the water in the lake is indicated by the trend of the principal currents. It has been found that the currents of the Laurentian Lakes have in general a speed of from four to twelve miles a day, but in certain observed instances this is increased to two and one-half to four miles per hour. When the currents follow the shore, important results in a physiographic sense may follow. When the wind blows obliquely to the shore strong currents are frequently produced which follow the general trend of the coast, but sweep across bays and inlets. These currents with the assistance of the waves sweep along sand and gravel and produce important changes in the bottom particularly where the water is shallow. The prevailing littoral current unaided is however, not strong enough to transport any considerable amount of coarser material and in a general way it may be said that the condition of the water is not as disturbed as in the Upper Ohio Drainage where a considerable amount of such material is carried along.

As a rule, the temperature of the water in Lake Erie is much cooler than that in the Upper Ohio Drainage. The shallow lakes of the Northern states have been found to have a nearly uniform temperature during the summer months of 75° F. (42). In the winter the temperature is generally 32° F. This condition has an important bearing upon the growth of *Naiades*. It is a well-known physiological fact that the rapidity of nutritive processes in "cold-blooded" animals depends largely upon the temperature to which they are subjected. Again the food of the *Naiades* consists largely of plankton.

I quote from a letter from Mr. A. F. Shira, Director of the Biological Station at Fairport, Iowa, "It may be said that an increase in the temperature of a lake favors an increase in plankton, and there is an increase in plankton during the spring and in early summer followed generally by a decrease in autumn. Temperature affects the character

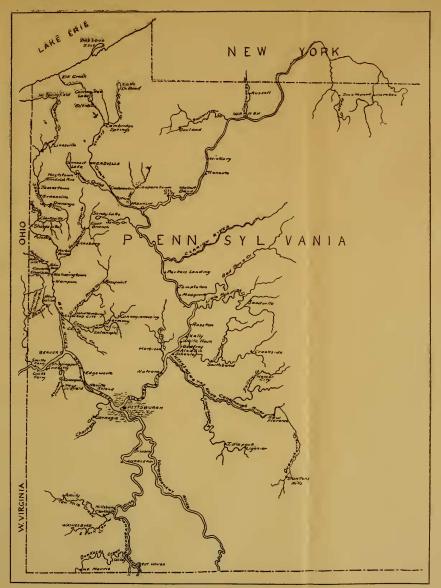






Map Illustrating Sources of Material Discussed by N. M. Grier.





Map Giving Localities Mentioned by N. M. Grier.



as well as the quantity of plankton. A low temperature favors the increase and development of diatoms, while a high temperature favors especially the development of water bloom algæ, also such forms as *Vorticella*." Allen (2) claims that other algæ than diatoms form fully as large a part of the food, and lists more species of these from the digestive tract of *Naiades* than diatoms (63). The colder waters of Lake Erie would therefore tend to inhibit the growth of those forms of algæ except diatoms, even in the summer months.

With the following extract from Kofoid (27) the question of plankton as a source of food for *Naiades* may be dismissed. "Stream plankton differs from all others in the mingling of plankton from all sources, and in being subject to variation in quantity. It appears to be more subject to catastrophic change than that of the lake, possibly on account of the conditions just described. Changes in the volume of the water, the contact of shore and bottom, access of heat and light, and changes in chemical composition are frequently more extensive and more widely effective in streams than in other types of aquatic environments." Kofoid believed Chlorophycea were somewhat more characteristic of the plankton of rivers than of lakes. Silt (there is more of this in the river) is supposed to hasten the growth of plankton by providing its source of nourishment in an easily obtained form. It would follow in the writer's opinion that fluviatile Naiades, all factors considered, have a more abundant, if less regular, supply of food than those of the lakes. Perhaps the larger amount of silt received in the spring in the lakes accounts for abundance of plankton then, especially when coupled with the rising temperature.

Characteristics of the Mussel Fauna of Lake Erie.

The studies of Walker (54, 55) have shown that the Lake Erie fauna did not persist through the Glacial Period. Representative *Naiades* now found in the Great Lake Region of the Mississippi and Ohio Faunas are the result of post glacial invasion (47). It is Dr. Walker's opinion that to this is to be ascribed the present existence of so large a number of representatives of the Mississippi Fauna in Lake Erie. This migration may be traced at one end of the lake through the Maumee Outlet into the post glacial Lake Maumee; at the other end the ancient headwaters of the Ohio tributaries once emptied (28). Walker ascribes the modifications which have taken place in their size, shape, and appearance to the environmental changes which have occurred since glacial time, more particularly in temperature. In addition he points out that the Naiades of the warm waters in the interior of the state of Michigan attain the same size, luxuriance of growth, and color as they do at the present time in the Mississippi and Ohio Valleys, although their ancestors originally came from the lake. There is, on the other hand, some evidence for believing that they may have come from northern Indiana through an ancient pre-glacial drainage (47), and another way of attacking the problem with which we are dealing, were material sufficiently abundant, would be to compare the shells of the interior waters of Michigan with those of Lake Erie. Lake Erie shells are characterized by brighter colors, when compared with their silt- and iron-stained fellows of the rivers, are exceptionally polished, and characterized otherwise in distinction by their well developed lines of growth. Dr. Walker in a letter to the writer (1914) suggested that a possible source of the depauperate quality of the shells may be the chemical quality of the water itself, pointing out that the influence of brackish water upon fluviatile species is well known, and there is no good reason why the infusion of the other materials than those in the rivers should not have their influence for good or bad in the same way. An analysis of Lake Erie water furnished through the courtesy of Mr. J. S. Dunwoody, Superintendent of the Filtration Plant at Eric, Pa., is given below, for comparison with that of the Upper Ohio Drainage at Pittsburgh, Pa. (29).

Analysis of water of Lake Erie at Erie, Pa.	Parts per million.		Analysis of water at Pittsburgh, Pa. Parts per million.
Turbidity	3-100		55
Color	30-40	*	122
Iron	very little		2
Alkalinity	105		47.4
Calcium carbonate	90		56
Magnesium carbonate	18		*
Magnesium sulfate	25.5		*
Calcium sulfate	a little		20
Sodium and potass. chlorides	21.8		26
Sodium and potass. sulfat es	30		20

These analyses are corroborative of certain statements I have made, and furnish food for reflection.

* These substances are not recorded as being present in the water at Pittsburgh.

Physical Conditions of the Drainage Basin of the Upper Ohio.

The drainage basin of the Upper Ohio River (19, 28, 44) lies in the central part of the eastern part of the United States. The river is formed by the junction of the Allegheny and Monongahela Rivers at Pittsburgh, Pennsylvania. From that point the Ohio flows in a generally southwestern direction and joins the Mississippi at Cairo, Illinois. The principal tributaries with which this investigation is concerned (beginning at the source and following down the right or north bank) are the Allegheny and Beaver Rivers; on the left are the Monongahela River, Raccoon Creek and Chartiers Creek. The total length of the Ohio River is 767 miles and the total area drained is about 210,000 square miles. The portion of the drainage basin with which we are concerned lies in the states of New York, Pennsylvania, Ohio, West Virginia, and Maryland. The source of the tributaries from the north lies in the glaciated area, the sources of the southern tributaries are located in the steep and rocky slopes of the western side of the Appalachian Mountains. The topography varies from flat and rolling in the western and northern portions, to rough and mountainous in the southern and eastern sections.

The Allegheny River, which unites with the Monongahela River at Pittsburgh to form the Ohio, drains the western slopes of the Allegheny Mountains. The Allegheny is the larger stream, as its drainage area is nearly fifty per cent. greater than that of the Monongahela. The drainage of the Allegheny lies in the states of Pennsylvania and New York. The river rises in the central part of Potter County in the northern part of Pennsylvania; flows in a generally northwestern direction across the state line into New York, thence southward back into Pennsylvania. At Franklin in Venango County the river turns and flows southeastward to the mouth of Mahoning Creek in Armstrong County, thence it turns to the southwest and joins the Ohio at Pittsburgh. The upper Allegheny and its tributaries are plateau streams, originating upon the Allegheny plateau at an elevation of 300 feet above the main stream. The tributaries above the Clarion descend by rapids and cascades from only a height of 150 to 200 feet above the river.

The tributaries with which we are concerned beginning at the source and following down the right bank as follows: Conewango, Brokenstraw, and French Creeks; on the left bank are Potato Creek, Clarion River, Red Bank, Mahoning, and Crooked Creeks, and the Kiskiminetas River. The total length of the river is about 200 miles. and the total drainage area 11,000 square miles. The surrounding country is extremely rough and broken, being made up of high hills or mountains separated by deep valleys. As the limits of the basin to the west of the main river are approached, the mountainous character is lost, although the surface is still rolling and hilly. The bed of the stream is composed chiefly of glacial gravel, varying from small pebbles to cobblestones. The Allegheny River descends from an elevation of 2500 feet above tide at Olean, New York to 707 feet above sea-level at Pittsburgh, Pennsylvania. In the last eighty-two miles of its course its descent averages two feet per mile. In the region of the headwaters of the Allegheny, as well as in all streams we are dealing with, erosion is going on rapidly (4, 37) which is indicated by frequent falls and rapids (riffles), and no, or only short, stretches of quiet pools. A load of debris is carried, which moves quickly over the bottom. Further down at the maturity of the rivers, rapids become scarce, quiet pools are more numerous, and although the water moves somewhat rapidly in these it is with a steady uniform current. Mussels developed under the conditions described for the region of the headwaters are those we are comparing with those from Lake Erie, and are characteristic of the various small tributaries seen on the map. We are concerned with the tributaries of the Monongahela and Ohio River rather than with those streams themselves.

The conditions surrounding the affluents of the Monongahela and those entering the Ohio from the south are much the same as those of the upper Allegheny and its tributaries and we need only mention Raccoon and Chartiers Creeks flowing into the Ohio, and Cheat River, Dunkard, and Ten-Mile Creeks, tributaries of the Monongahela, as sources from which our material has been derived.

Drainage Basin of the Beaver River.

The Beaver River is formed by the junction of the Shenango and Mahoning Rivers in western Pennsylvania and flows southeasterly twenty-two and one-half miles to the Ohio River. Above New Castle its basin lies in the glaciated area, containing broad valleys with many swamps and ponds. The main valley as far as Wampum is broad with wide flat bottom-lands. The principal tributaries are the Connoquenessing and Slippery-rock Creek. The Shenango River, a tributary, arises in northwestern Pennsylvania, and flows eighty-seven and one-half miles through the glaciated area, where are many swamps and small lakes, and the country is generally broad and flat, to its junction with the Beaver. The principal tributaries are Pymatuning Creek, Little Shenango River, and Neshannock Creek. The Mahoning River arises in Ohio, flowing twelve miles in Pennsylvania to its junction with the Shenango to form the Beaver. Its course is through broad valleys and rolling hills in the glaciated region. The majority of these streams are of comparatively recent (glacial) origin.

Characteristics of the Naiad Fauna.

The fauna of the Ohio River (37) and tributaries is that of the interior basin and is largely post-glacial in origin, having migrated up stream in post-glacial times. The most conclusive evidence points to its original source as having been in the drainage of the Tennessee River. The fauna may be traced from the Licking River up through the whole Upper Ohio Drainage into the headwaters of the Allegheny and the Monongahela. As a whole it may be considered a somewhat depauperate Tennessee fauna (37) becoming (although richer and more exuberant than that of Lake Erie), more greatly so in the rivers above Pittsburgh, in the Allegheny and its tributaries to a greater extent than in the Monongahela and its tributaries. In the latter and its tributaries the rich Ohio fauna, only slightly depauperated, goes up to a certain point at the lower end of canyons where begin extremely rough portions of the rivers. The species of shells found in the Monongahela, but not the Alleghenv, are pre-eminently "big river forms" while those of the Allegheny are those of a small river. The Beaver River is a glacial drift stream. Wetherby remarks (58) "It is a significant fact that those North American rivers which contain the richest Unione Fauna drain Mesozoic and Tertiary regions, while those that drain Paleozoic and Azoic regions have a comparatively meagre Unione Fauna."

Summary of the Physical Conditions in Lake Erie and the Upper Ohio Drainage which affect the Naiades.

Lake Erie resembles "big streams" in having the sandy and gravelly bottom, preferred by Mollusca. The shells are not subject to the agitation of the water occurring in the streams, as is shown by the well preserved condition in which they are collected. While the water is colder, it is clearer; there is a more even temperature. Streams in summer may nearly dry up, or in winter become solidly frozen. Such conditions do not occur in Lake Erie. The effect of this environment is shown in the *regular growth lines* of the shells and their brighter colors. On the other hand the waters of the Upper Ohio Drainage are usually warmer, contain less lime, and the food conditions are less stable, if even at times food is more abundant.

V. The accompanying table giving the list of localities at which collections were made, will give some idea of the distribution of the species employed in this research.

VI. METHOD OF MEASUREMENT.

A careful selection was first made of the material on hand to eliminate all stunted or otherwise abnormal specimens. The following data were then recorded from usually the right valve of each animal:

- Length = L. With vernier caliper. (Scientific Materials Company Catalog No. 3930.)
- 2. Dorso-ventral diameter = D.V.D. With vernier caliper.
- 3. Dextro-sinistral = D.S.D. With vernier caliper.

4 and 5. Distances anterior; (AD), and posterior, (PD, from DVD) to extremities of valve, (the sum giving total antero-posterior dimension), length, D, of shells, with a modification of the stadiometer used by Davenport in his studies on "Evolution of Pecten" (13).*

* The stadiometer as made by the writer consisted of a nearly circular box-like base of sheet-iron about fourteen inches in diameter and one-half inch in width. one end of which was squared. To this end in the cavity of the box was soldered in an inverted position the upper jaw of a vernier caliper like that already mentioned, so that the zero-point coincided with the upper surface of the box. The upper jaw of the caliper was free to move up and down the graduated seale. On the upper surface of the box there was then pasted metrically ruled paper, and a zero-point established to coincide with the zero-point of the caliper, after which the centimeter spaces were numbered to the right, to the left, and to the opposite end of the instrument. In using the instrument it was the custom to take the most convenient valve of the mussel, place it upon the base of the instrument with the umbo, or its probable location, as far as could be determined, on the zero-point. Dimensions AD and PD could be readily taken, and if desired, DVD, and by manipulation of the free arm of the caliper until flush with the surface of the valve, one-half of the dextro-sinistral diameter from the graduated arm of the caliper.

coccinenn. ferussacianus. Eurynia vecta latissima. Pleurobema obirquum Paraptera fragilis. Lasmigona costata. grandis. Lampsilis Inteola. Amblema costata. dilatatus. Fusconaja flava. List of Localities. nodontoides Anodonta , Proptera Elliptio ΝI IA III 1 5 2 DRAINAGE OF UPPER OHIO RIVER. I. Potato Creek, Smethport..... * ж * * * 2. Allegheny River, Larabee..... * * * . . * * * 66 Warren..... * 3. * * sk * 4. Conewango Creek, Russell...... h . . 5. Allegheny River, Hickory..... * * * * 6. Brokenstraw Creek, Garland * * * * * * ж . * * * * . . 9. Sandy Creek..... . . * 10. Allegheny River, Parker's Landing \mathbf{v} * * * sk × 66 Templeton...... sk II. " * ж x Mosgrove..... * sk τ2. 6.6 66 Rosston..... * * * * * * * 13. * * ... Kelly..... * * 4 ... * * 20 sk: 14. Godfrey..... * * * Johnetta..... * * ... 6.6 * * * 15. * * 66 ж * * ж * т6. ... Aladdin * * * * 17. * * * * 4 * * 6.6 20. Natrona * 21. Harmarville Pond..... DRAINAGE OF FRENCH CREEK. 22. Le Boeuf Creek...... * * * * * * * 23. Cambridge Springs..... * * * * * * * × * * * 25. Conneauttee Creek.....* * * * 26. Meadville * ... * * * * 27. Conneaut Lake..... * N.E. Shore * * 28 . . * 6.6 29. * . . * * * * * *

 34. Sugar Creek, Cooperstown
 ...
 *
 *

 35. Little Mahoning Creek, Goodville
 ...
 *
 ...

. . . * * *

TABLE I.

				ine un.									Ĩ.
	I Fusconaja flaza.	II Amblema costata.	III Pleurohema oblicaum coccineum	IV Elliptio dilatatus.	V Lasmigona costata.	VI Anodonta grandis.	VII Anodontoides ferussacianus.	VIII Paraptera fragilis.	IN Proptera lata.	X Eurynia rocta latissima.	XI Lampsilis Inteolu.	XII Lampsilis ovata ventricosa.	
			-	-		-	-	-		-	-	-	
36. Creek 37. South	DRAINAGE OF CROOKED CREEK. side Bend on.	* * *	••• •••		*		•••		•••	 	*	 	* * *
0	AINAGE OF KISKIMINETAS RIVER.												
39. Yellov 40. Quem 41. Coner	v Creek, Homer ahoning Creek, Stanton's Mills naugh River, New Florence hanna River, Ligonier	•••	•••	* *	* * .*	* : :*	· · ·	· · ·			· · ·	•••	· · · · * *
Dr.	AINAGE OF MONONGAHELA RIVER.												
45. Dunk 46. " 47. Ten-M 48. " 49. "	River, Cheat Haven ard Creek, Mt. Morris "Wiley file Creek, Waynesburg "Amity "Clarksville "Clarksville "Charleroi "Charleroi "Westmoreland Co	*		*	*	* * * * * *	*		*	*		** **	* :** ::*:
52. 53.	" " Elizabeth					*						*	*
54. Chart	" Edgeworth	*	 	· · · · · · · · · · · · · · · · · · ·		*		· · · ·			*	*	* * * * *
	DRAINAGE OF BEAVER RIVER.												
61. Rando	Jph Run, Hartstown ngo River, Jamestown " Greenville " Shenargo	· · · · · · · · · · · · · · · · · · ·	* * * *	*	* * * *	* * * *	*	* *		· · ·		• •	* * * *

TABLE I.—Continued.

TABLE I.—Conti	11 11	eu.										
List of Localities.	I Fusconaja flava,	II Amblema costata.	II Pleurobema obliquum coccineum.	IV Elliptio dilatatus.	V Lasmigona costata.	VI Anodonta grandis.	VII Anodontoides ferussacianus.	/ 111 Paraptera fragilis.	IX Proplera alata.	X Eurynia recta latissima.	XI Lampsilis luteola.	XII Lampsilis ovata ventricosa.
			_			_	_	-	_		_	
DRAINAGE OF BEAVER RIVER												
69. Pymatuning Creek, Pymatuning Twp		*	*	*	* *		*	• •		• •	*	*
70. Otter Creek71. Neshannock Creek, Leesburg	• •	• •	 *	· · *	*	•••	• •	• •	• •	• •	*	*
72. " " Eastbrook	•••		*	*			•••					*
73. Mahoning River, Leavittsburg, O						• •				• •	*	• •
74. " Edinboro 75. " Hillsville		*	 *	• •	• •	*	• •	• •	• •	• •	*	• •
75. " " Hillsville 76. " " Coverts		*	*	*	: *	•••	•••	•••	1			*
77. " " Mahoningtown		*		*								*
78. Beaver River, Wampum	*	*	*	*	* *	*	• •	• •	• •	• •	 *	*
79. Wolfe Creek, Grove City80. Slippery Rock Creek, Rose Point	Ť	••	Ŧ	••	*	Ť	• •	• •	••	• •	*	*
81. " " " Wurtemburg		*	*	*								*
82. Connoquenessing Creek, Elwood City		*	• •									*
83. "Harmony		• •	*	*	• •		• •	• •	• •	• •	• •	* ·
84."Zelienople85.Brush Creek, Celia	• •	• •	*	*	• •	*	• •	• •	• •	•••	•••	••
86. Little Beaver Creek, Cannelton				*							*	*
87. "" " Darlington			• •	*	*	• •					*	*
oo.	 *	• •	• •	*	*	• •	• •	•••	• •		•••	Ŧ
89. Raccoon Creek, New Sheffield		*	•••		*			•••			*	*
91. " " Industry		*			*			*	*	*		
92. " " Cook's Ferry		*	• •		*			*	*	*	*	*
93. "" " Smith's Ferry	• •	• •	• •	• •	*	•••	• •	*	*	•••	• •	Ť
Lake Erie.												
94. La Plaisance Bay	*	*	*	*	*	*		*	*	*	* *	*
95. Cedar Point 96. Vermilion, Ohio	*	*	•••	*	•••	*	• •	*	*	*	4	*
97. Presque Isle Bay		*	•••	 *		*	*		*			
98. Presque Isle, Beach-pools						*	*				*	•••
99. "" " East end, outer beach	 *	 *	• •	*	• •	• •		• •	•••	• •	•••	 *
100."East end, south shore101.""Flats near west end	*	Ŷ	• •	 *	*	 *	• •	*	*	 *	 *	*
102. " " Big Bend	*	*		*	*	*	*	*	*	*	*	*
103. " " " " W. of Waterworks.	*	*	*	*		• •	*	*	*	*	*	*
104. " " Misery Bay		*		*	*	*	• • •		*	• •		• •

TABLE I.—Continued.

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		2.	vleurobema oblicum soccincum.	45.	uta.	lis.	russacianus.	ilis.		atissima.	la.	ventricosa.
List of Localities.	Fusconaja flava.	Amblema costata.	Pleurobema obl.	Elliptio dilatatus.	Lasmigona costata	Anodonta grandis.	Anodontoides ferussacianus.	Paraptera fragilis.	Proptera aluta.	Euryma recta latissima.	Lampsilis Inteola.	Lampsilis ovata ventricosa
	Ţ	Π	III	IV	Δ	Γl	NII	IIIA	IX	X	IX	HX
LAKE ERIE. 105. Presque Isle, Crystal Point 106. ""Horseshoe Pond 107. Buffalo, New York 108. Port Colborne 109. Port Dover 110. Port Rowan DRAINAGE OF MAUMEE RIVER.		•••		*				*	· · · · ·	· · · · · · · · · · · · · · · · · · ·	***	* * : : * * *
111. St. Mary's River, Rockford112. Blanchard River, Finley113. Silver Creek, Williams County114. Maumee River, Rapids Station115. " " Pond116. " " Allen County, Ohio117. Miami and Erie Canal118. Ten-Mile Creek, Silica, Ohio119. St. Joseph's River, Ohio	*	•••	 	· · · · · · ·	· · · · · · · · · · · · · · · · · · ·	* * * • • • •	* * * .	• • •	*	· · · · · · · · · · · · · · · · · · ·	****	* * *
STREAMS DRAINING INTO LAKE ERIE. 120. Raisin River, Adrian Co., Mich 121. Otter Creek, Monroe Co., Michigan 122. Conneaut Creek, West Springfield 123. Elk Creek, Miles' Grove	•••		 *	•••			* * * *		•••	•••	*	* :*

TABLE I.—Continued.

6 and 7. Length of anterior (AHL) and posterior (PHL) part of the hinge measured from the beak, giving the total hinge-length, by means of a steel-rule. (Scientific Materials Company Catalog No. 3946). Where the hinge-line curved, it was possible with practice to estimate the length.

8. Thickness of the valve just superior to the pallial line, in the region directly beneath the umbo. It was thought that such a measurement might be more easily correlated with the other dimensions taken. This was secured with a micrometer-screw caliper. (Scientific Materials Company Catalog No. 3934.)

The above measurements were resolved to factors for comparison by division with the length, with the exception of the thickness of the shell, which it seemed desirable to compare with the dextrosinistral diameter, as giving more of a biological balance to this measurement, making it independent of any extraneous physical condition which might be involved. To facilitate the work of calculation, a Mannheim slide-rule was used, since the writer found by checking with calculations made by long hand that he was able to secure a fair degree of accuracy. Computations were usually made to the fourth place.

In recording the data thus obtained, it was found convenient to use a standard figuring book of twelve columns, double-page form, obtainable from most stationers. This provided ample space for any comments to be attached to any particular group. In comparison, the shells were first grouped into their respective drainages, after which the calculated data for the different localities were arranged in the order from headwaters to mouth of stream, and in the lake region from east to west. (See accompanying map, Pl. I.) Since the problem had to adjust itself to the amount of material on hand, it was not always possible to compare as large a number of shells as desirable from some localities. The smallest number was three, but since the results obtained consist of the average for the most part of a fairly large number of shells they are thought to reasonably justify the results obtained. The procedure was ordinarily to compare equal numbers of shells in each case. The kinds of comparison were as follows:

I. Comparison of *Naiades* of Lake Erie with their representative species in the streams entering the lake, principally the Maumee Drainage.

2. Comparison of these species of Lake Erie with their representative species in the streams of the Upper Ohio Drainage (Upper Allegheny and tributaries, Beaver and tributaries, etc.), as close as possible to the divide. Species from the latter drainages were at the same time compared with those of the Maumee.

The physiographical and geological considerations leading me to make my comparisons under these two heads are found in the sections dealing with "Physical Conditions" and "Characteristics of the Mussel Fauna." It is true that in Pennsylvania few or none of the shells have gone over into the lake, yet excellent authority states that the shells of the Upper Ohio resemble in a striking way those of the lake tributaries in Ohio, and living under similar conditions. It seems that no serious mistake will be made if this is done, for there is no evidence to show that post-glacially the shells have become extremely modified. Moreover the shells from the Maumee are comparatively few in number.

If I am asked why on the other hand only specimens from streams nearest the divide are considered, it will be clear from the literature quoted, and substantiated by the opinion of excellent systematists that in the lower stretches of the Upper Ohio Drainage "big stream" conditions have so modified and are so modifying the *Naiades*, that it would be extremely difficult, if possible, to use the *same species* in a number of cases. In others, however, a paucity of material, where there is reason to believe the species is not excessively varying, has led to the utilization of material from larger streams.

VII. RESULTS.

The values obtained from these calculations are found on Table IV. For the convenience of the writer as well as of the reader the comparisons derived were then tabulated as shown in Table III from which all written conclusions are derived. Table II gives the maxima, minima, and mean of all dimensions for each species of shell from the two environments, affording closer insight into Table III. The actual measurements of the shell from which the material in Tables II and III is derived, while really belonging here, are placed at the end of the paper for the sake of convenience.

VIII. CONCLUSIONS.

The outstanding facts to be gathered from Tables II and III are:

I. All shells, with exception of *Anodontoides ferussacianus* obtain a greater degree of inflation in Lake Erie than in the Ohio. It follows from this and other evidence, which I have presented, that shells are longer in the Upper Ohio.

2. The height of a shell (DVD), appears to be indifferently influenced by either environment according to these measurements, although it could be stated that most species tend to be "higher" in the Upper Ohio and the tributaries of Lake Erie.

3. The evidence shows that the great majority of species tend to have a greater posterior development (PD), in Lake Erie, and greater anterior development (AD) in the Upper Ohio, etc.

48 34 38 38 38 20 10 20 \$14 80 80 80 5.3 4.5 .xelv 14ΙI .d.1d 3.5 II 13 01 30 32 II I 2/Isah 31 34 48 47 SHOWING MAXIMA, MINIMA, AND MEAN (RANGE OF VARIATION EXPRESSED IN PERCENTAGES) OF CERTAIN MUSSELS 14 12 14 14 16 is is a 9 9 9 20 48 $\pm \infty$ 0 0 0 ·uiIV 2 91 01 00 8 26 30 00 28 30 32 22 22 26 26 30 26 26 28 54 .xsM 24 18 OF THE UPPER OHIO DRAINAGE. . THF 21 15 17 21 21 20 .nssM 28 2 I 21 4014401 10144010 14 UIIV 98 62 64 52 .xsM 56 64 66 64 PHL223 12 Mean +++ 38 .uilt .xeW GF T 3030 ns51/ 27 9 20 20 18 12 18 2 2 2 $\mathbf{I}_{\mathbf{S}}$ 18 ti 2 2 2 t 1 'uilv INHABITING LAKE ERIE COMPARED WITH CORRESPONDING MUSSELS 780 78 80 .xeI/ DD. 772888774 Mean 00 58 64 64 . ui IV 1- 09 60 66 8 5 5 5 40 86 86 10 58 66 92 44 5 00 88 $^{84}_{83}$.xeM DUD20 .nssM 50 64 64 64 62 62 66 30 56 56 'uily 64 .xsM 3 62 $\frac{DSD}{L}$. 20 Mean. 49 33 31 31 37 27 28 Ŧ 38 SI 41 26 .uil/ <u></u> 30 28 42 42 5 24 20 28 28 24 32 28 30 200 200 5 24 32 28 38 38 Ohio Ohio Ohio Ohio Ohio Ohio Ohio Ohio Ohio Erie Ohio Erie Ohio Erie Erie Erie Erie Erie Erie Ohio Erie Erie Erie Erie Locality. 515 3 Ι. Ľ. чы Ŀ. Ľ. No. of Speci-12 43 21 20 20 $^{2\,\mathrm{I}}$ 21 15 52 99 00 12 19 19 29 2 I15 999 52 E. dilatatus sterkii..... Sympliynola costata Amblema plicata..... parvula P. obliq. pauperculum Pleurobema obliquum coccineum Fusconaja flava..... S. costata eriganensis..... Eurynia recta..... E. recta latissima Anodonta grandis. A. grandis var. fooliana . . . Anodontoides ferussacianus. Elliptio dilatatus Paraptera fragilis A. feruss. subcylindricus. Lampsilis luteola Lampsilis ovata.... Mussel.

TABLE II.

Annals of the Carnegie Museum.

TABLE III.

Giving Results of Comparison of Values for Each Dimension in the Two Environments.*

$\frac{DSD}{L}$

(Dextro sinistral diameter, or convexity, divided by length giving degree of inflation.)

Greater Value Ohio Dra		Species with Eve	n No. Cases.	Greater Value in	L. Erie.
A. ferussacia	nus (4)			Fusconaja	(5)
				Amblema	(2-3)
				Pleurobema	(5)
				Elliptio	(4)
				Symphynota	(2)
				Anodonta	(4)
				Paraptera	(2)
				Proptera	(4)
				Eurynia	(2)
				L. luteola	(3)
				L. ovata	(4)
		DV.	D		
		L	_		
(Dorsa	al ventral dia	umeter of value or	its "height,"	divided by length	.)
Greater Value Ohio Drai		Species with Eve	n No. Cases,	Greater Value in	L. Erie.
Amblema	(3)	Elliptio	(2)	Fusconaja	(5)

Ohio Drainage.		Species with Even N	No. Cases.	Greater Value in L. Erie.		
Amblema	(3)	Elliptio	(2)	Fusconaja	(5)	
Pleurobema*	(3-5)	Symphynota	(1)	Proptera	(3-4)	
Anodonta	(4)	Paraptera	(1)	L. ovata	(4)	
L. luteola	(3)	A. ferussacianu	is (2)			
		Eurynia	(1)			

$\frac{PD}{L}$

(Distance posterior to extremity from a line passing through median dorso-ventral plane of value.)

Ohio Drai		Species with Even	No. Cases.	Greater Value in	L. Erie.
Eurynia	(2)	Proptera	(2)	Fusconaja	(5)
L. ovata	(3-4)	Paraptera	(2)	Amblema	(3-4)
		A. ferussacian	<i>ius</i> (2)	Pleurobema	(4-5)
				Elliptio	(4)
				Symphynota	(2)
				Anodonta	(4)
				L. luteola	(3)

* Number of cases in which this occurs is given after name of each species—2-3 etc. means 2 cases out of 3, etc. In species with even number of cases, number is given after each.

TABLE III.—Continued.

ADL

(Distance anterior to extremity from a line passing through median dorso-ventral plane of value.)

Ohio Drainage.		Species with Even	No. Cases.	Greater Value in L. Erie.				
Fusconaja	(5)	Proptera	(2)	L. ovata	(3-4)			
Amblema	(3)	Paraptera	(1)					
Pleurobema	(4-5)	Eurynia	(1)					
Elliptio	(4)							
Symphynota	(2)							
Anodonta	(4)							
A. ferussacianus	(3-4)							
L. luteola	(3)							
		$\frac{PHL}{L}$	-					

(Length of shell compared with posterior hinge-line.) Greater Value in Upper

Ohio Drainage.		Species with Ever	No. Cases.	Greater Value in L. Erie.			
Proptera	(4)	L. ovata	(2)	Fusconaja	(4-5)		
Eurynia	(2)	Paraptera	(1)	Pleurobema	(3-5)		
				Amblema	(3)		
				Elliptio	(3-4)		
				Symphynota	(2)		
				Anodonta	(4)		
				A. ferussacianu	s (3-4)		

AHL

L

L. luteola

(2-3)

(Length of shell compared with anterior hinge-line.)

Greater Value in Uppe Ohio Drainage,	Species with Even	No. Cases.	Greater Value in L. Erie.		
Fusconaja (4-	5) Pleurobema	(3)	Proptera	(4)	
Amblema (3)	Paraptera	(1)			
Elliptio (3-	-4) Eurynia	(1)			
Symphynota (2)	L. ovata	(2)			
Anodonta (4)					
A. ferussacianus (4)					
L. luteola (2-	07				
	TH				

\overline{DVD} (Thickness of shell divided by dorso-ventral diameter.)

Greater Value i Ohio Drain		Species with Eve	n No. Cases.	Greater Value in	L. Erie.
Amblema	(2)	Elliptio	(2)	Fusconaja	(3-5)
Pleurobema	(3-5)	L. ovata	(2)	Anodonta	(4)
Proptera	(4)			Paraptera	(2)
A. ferussacian	us (3–4)				
Symphynota	(2)				
Eurynia	(2)				
L. lutcola	(2-3)				

TABLE IV.

ACTUAL MEASUREMENTS OF SHELLS USED IN A COMPARISON Fusconaja flava parvula, Lake Erie.

	No. Spec.	$\frac{DSD}{L}$.	$\frac{DVD}{L}.$	$\frac{PD}{L}$.	$\frac{AO}{L}$.	$\frac{PHL}{L}.$	$\frac{AHL}{L}.$	$\frac{TH}{DVD}$
Lake Erie, La Plaisance Bay	4	,5237	.7717	.794	.1946	.515	.1840	.123
Lake Erie, La Plaisance Bay	7				.2197			-
Lake Erie, Cedar Point	4				.2046		.1592	
Presque Isle Bay, Various Lo-		501		.,,=5		.4-5		,
calities	-1	.518	.8131	.702	.212	.574	.2301	.110
Presque Isle Bay, Various Lo-	7			.1)-		.514		,
calities	7	.5.15	.8205	.703.1	.301	.40.1	.1838	.121
Maumee River Drainage, Mi-	'	-545	10=95	1954		1.40.4	11030	
ami & Erie Canal, Allen Co.,								
etc	4	.473	7 107	765	220	552	2786	TTT8
	4	.475	.1491	.105	.239	.333	.2700	.1110
Fusconaja flava, Compariso	on Upi	PER OF	110 Dr	AINAG	E WITH	I LAKE	ERIE	
Allegheny tributaries (36-38).	27	.4481	.7663	.7175	.2740	.4901	.3150	.1175
Lake Erie (98, 99, 102)	27	.544	.8492	.781	.2318	.529	.2154	.1140.
Allegheny River (13-14)	13	.4650	.7678		.2712			
Lake Erie (98, 99, 102)	13		.788			.522		P
Lake Erie (102-119)	16	.551	.8827		.2439	~	.2396	
Monongahela tributaries (44-		.55-			- 455	. 5 +=		
49)	16	.175.1	.7060	.7362	.2793	.1870	.225.1	.108.1
Ohio tributaries (54)	12				.2563		0.1	
Presque Isle (102–119)	12				.2755			
a resque tote (res ing)		.559	10 144	.153		.520		

COMPARISON Amblema plicata, LAKE ERIE DRAINAGE.

La Plaisance Bay, Lake Erie Sandusky Bay, Cedar Point			.1700		
		 0	.1784	0 -	

Amblema costata, Comparison Upper Ohio Drainage with Lake Erie.

La Plaisance Bay, Cedar Point								
(98-99)	I 2	.444	.757	.829	.1793	.595	.1834	.1173
Presque Isle (101-120)	12	.426	.762	.816	.1823	.564	.1767	.1393
Presque Isle (101–120)	15	.436	.7689	.818	.1787	.565	.1784	.1373
Allegheny River (12–17)	15	.4391	.7688	.810	.1812	.607	.1885	.1495
Presque Isle (101–120)	15	.436	.7689	.818	.1787	.565	.1784	.1373
Allegheny tributaries (22, 23,								
26, 31–33)	15	.3908	.7777	.760	.2364	.579	.2032	.1506
Presque Isle (101–120)		.435	.7719	.819	.1758	.569	.1774	.1385
Beaver tributaries (60-78)		.408	.7756	.760	.2332	.587	.1894	.1504
Presque Isle (101-120)			.7613		.1820	.566	.1830	.1348
Beaver River (79)	7	.459	.7667	.741	.256	.552	.2119	.1647

COMPARISON Pleurobema obliquum pauperculum, LAKE ERIE DRAINAGE.

La Plaisance Bay	3	.468	.758	.897	.103	.619	.1262 .0964
Big Bend	3	.477	.662	.857	.1945	.573	.1828 .1175

TABLE IV.—Continued.

Pleurobema obliquum coccineum, Comparison Upper Ohio Drainage with Lake Erie.

	No. Spec.	$\frac{DSD}{L}$.	$\frac{DPD}{L}.$	$\frac{PD}{L}$.	$\frac{AD}{L}$.	$\frac{PHL}{L}.$	AHL L	TH DVD'
Presque Isle, Lake Erie, etc.								
(101–119)		.468	.731	.871	.1284	.591	.1850	.1146
Allegheny tributaries (4, 16,								
18, 35)	I 2	·45I	.832	.822	.1755	.583	.2008	.1359
Presque Isle (101–119)	I 2	.468	.731	.871	.1284	.591	.1850	.1146
Beaver Drainage (79, 62-78)	I 2	.459	.757	.873	.1264	.605	.2422	.1060
Presque Isle (101–119)	I 2	.468	.731	.871	.1284	.591	.1850	.1146
Allegheny tributaries (22-34)	12	.426	.806	.8372	.1627	.546	.1873	.1271
Presque Isle (101–119)	I 2	.468	.731	.871	.1284	.591	.1850	.1146
Beaver River (79)	I 2	.435	.648	.823	.1811	.468	.1708	.1379
Presque Isle (102–119)	I 2	.468	.731	.871	.1284	.591	.1850	.1146
French Creek (22–34)	I 2	.432	.805	.8457	.1540	.547	.1934	.1350

COMPARISON Elliptio dilatatus sterkii, LAKE ERIE DRAINAGE.

Lake Erie, La Plaisance Bay.	6	.3159	.525	.826	.1674	.576	.1504	.1225
Presque Isle Bay	6	.315	.494	.806	.188	.560	.1333	.1071

Elliptio dilatatus, COMPARISON UPPER OHIO DRAINAGE WITH LAKE ERIE.

La Plaisance Bay (98)	6	.3159 .5	25 .826	.1674 .576	.1504 .1225
Presque Isle (101–120)	6	.315 .4	94 .806	.188 .560	.1333 .1071
Presque Isle (101-120)	31	.3119 .4	98 .807	.187 .542	.1656 .1025
Allegheny tributaries (22–34).	31	.283 .4	96 .778	.2196 .521	.2093 .1128
Presque Isle (101–120)	31	.3119 .4	98 .807	.187 .542	.1656 .1025
Beaver Drainage (60–79)	31	.283 .5	01 .768	.2316 .5381	.1898 .0993
Presque Isle (101–120)	31	.3119 .4	98 .807	.187 .542	.1656 .1025
Allegheny River (5–20)	31	.2906 .4	917 .7825	.2503 .496	.1964 .1156
Presque Isle (101–120)	14	.315 .4	92 .808	.1204 .5400	.1077 .1320
Beaver River (79)	I.4	.2425 .4	575 .783	.215 1.507	.1591 .1461

COMPARISON Symphynota costata eriganensis, LAKE ERIE DRAINAGE.

Lake Erie, Monroe County,								
Mich	5	.307	.552	.764	.233		.1826	.0876
Presque Isle Bay	5	.354	.560	.763	.2.40	.540	.215	.0853

Symphynota costata, Comparison Upper Ohio Drainage with Lake Erie.

Presque Isle (99–120) Allegheny tributaries (22–34) Presque Isle, Lake Erie (101–		
120) Beaver Drainage (60–85)		

COMPARISON Anodonta grandis footiana, LAKE ERIE DRAINAGE.

Lake Erie, Cedar Point	5 3						.281	
Lake Erie, Presque Isle Bay	5	.383	.520	.752	.245	.446	.330	.1039
Maumee River, Roche LeBoeuf								
Rapids, Miami & Erie Canal	5	.388	.572	.732	.258	-377	.266	.0765

TABLE IV.-Continued.

Anodonta grandis, COMPARISON UPPER OHIO DRAINAGE WITH LAKE ERIE.

	No. Spec.	$\frac{DSD}{L}$.	$\frac{DTD}{L}.$	$\frac{PD}{L}$.	$\frac{AD}{L}$.	$\left \frac{PHL}{L} \right $	$\frac{AHL}{L}$.	$\frac{TH}{DTD}$
Tributaries, Lake Erie (139-							•	
140)	8	.383	.582	.743	.265	.378	.253	.0255
Presque Isle (99–120)	8	.396	.537	.747	.251	.441	.252	.0793
Presque Isle (99–120)	6	.402	.562	.734	.264	.442	.263	.0964
Monongahela tributaries (6, 9).	6	.345	.577	.727	.272	.380	.2584	.0620
Presque Isle (99–120)	14	.375	.551	.719	.278	.445	.2404	.0797
Allegheny tributaries (22, 34,								
45)	14	.372	.567	.695	.296	.384	.221	.0522
Presque Isle (139–140)	15	.367	.542	.765	.243	.449	.2442	.0833
Beaver Drainage (60-85)	15	.361	.557	.737	.260	.393	.229	.0549

COMPARISON Anodontoides ferussacianus, UPPER OHIO DRAINAGE.

Shenango River, Linesville Shenango River, Greenville,	6	.381	•543	.732	.271	.391	.242	.0518
Sharpsville	6	.360	.574	.708	.293	.319	.198	.0517

Paraptera fragilis, OHIO RIVER DRAINAGE.

Allegheny River: Kelly, God- frey, Aladdin Ohio River: Dead Man's Island	4	.333	.818	.772	.227	.562	.213	.0492
& Edgeworth	3	.312	.653	.736	.263	.417	.218	.0531
Ohio River: Beaver		.340	.680	.720	.283	.467	.225	.0500
Ohio River: Industry	5	.304	.707	.712	.294	.437	.1894	.0522
Ohio River: Cook's Ferry and								
Smith's Ferry	5	.325	.685	.742	.261	.469	.216	.0538
Ohio River	4	.305	.683	.727	.275	.469	.214	.0522

Paraptera fragilis, LAKE ERIE DRAINAGE.

Lake Erie, La Plaisance Bay	6	.315	.686	.739	.261	.543	.1970	.0517
Lake Erie, Presque Isle Bay	6	.322	.730	.764	.2430	.514	.1851	.0509

Paraptera fragilis, COMPARISON UPPER OHIO DRAINAGE WITH LAKE ERIE.

La Plaisance (98)	7	.316	.681	.743	.258	.535	.2003 .0515
Presque Isle (99–120)	7	.337	.735	.721	.281	.506	.2176 .0491
All Lake Erie (98–124)	20	.339	.716	.738	.263	.518	.2111 .0619
Ohio Valley (1-59)	20	.323	.708	.736	.265	.470	.2123 .0516
Presque Isle (101)	4	.361	.753	.726	.273	.514	.2059 .0495
Allegheny River (15–16)	4	.333	.818	.772		.562	.213 .0492

Proptera alata, LAKE ERIE DRAINAGE.

La Plaisance Bay La Plaisance Bay Cedar Point, Lake Erie Presque Isle Bay Maumee River, Roche de Boeuf	5 5	.329 .391	.850 .796 .811 .789	.723 .705	.273 .295	.525 .550	.1948 .2221	.0591 .0645
Rapids	5	.345	.654	.731	.267	.539	.1751	.094

TABLE IV.—Continued.

Prophera alata, Comparison Upper Ohio Drainage with Lake Erie.

	No	DSD	DVD	PD	AD	PHL	AHL	TH
	Spec.	L	L.	<u></u> .	ī.	L.	L ·	$\overline{D}\overline{P}\overline{D}^{*}$
Allegheny River (12, 14, 15)	8	215	7.40	712	.285	.563	2227	.0991
Presque Isle (99–119)	8	.345	.740 .789	.713	.205	.536	.2327	.0848
Ohio River (55–56)		·379 .310	.809	.664	.292	.558	.2142	
	14		-				.222	.0769
Lake Erie (99–102)	14	.404	.807	.709	.290	.555		
La Plaisance (98)	6	.315	.686	.739	.261	•543	.1470	.0517
Presque Isle (101–119)	6	.322	.730	.764	.2430		.1851	.0507
Presque Isle (101–119) Monongahela River (51)	4	.430 .314	.825 .766	.710 .668	.289 .330	·575 ·575	.226 .184	.0690
Comparison Anodontoides ferr								
COMPARISON A noaomotaes jera	15540.14	nus su	, ocyuna	ricus,	DAGE		DRAIN	10121
Lake Erie, Presque Isle	5	.366	.515	.719	.280	.413	.214	.0550
Maumee Drainage	5	.364	.566	.728	.268	.396	.233	.0626
Anodontoides ferussacianus, Com	PARISC	on Upp	er Oh	io Dr	AINAGE	WITH	LAKE	Erie.
Beaver tributaries (60–66, 62,	61			-				
	6	.374	.541	.721	.325	.381	.225	.0563
69) Presque Isle (99–120)	6				·345 .278			.0564
	8	.364	.513	.723		.412	.222	
Presque Isle (99–120)		.366	.511	.728	.272	.435	.223	.0572
Lake Erie tributaries (139–140)	8	.377	.576	.722	.276	.378	.229	.0514
Presque Isle (99–120)	7	.369	.517	.726	.274	.431	.227	.0538
French Creek Drainage (22–34)	7	.390	.630	.689	.320	.436	.2530	.0636
Presque Isle (99–120)	7	.369	.519	.726	.274	.431	.227	.0538
Beaver Drainage (60-85)	7	.333	.494	.728	.254	.336	.209	.0530
Presque Isle (99–120)	12	+334	.497	.675	.343	.406	.199	.0497
Shenango Drainage (61-69)	I 2	.370	.558	.720	.282	.355	.220	.0518
Eurynia r	recta, L	AKE E	rie D	RAINA	GE.			
La Plaisance Bay	2	.260	.40	.816	.184	.572	.1367	.1220
Cedar Point	3	.247	.375	.773	.226	.500		.1187
Presque Isle Bay	3	.267	.424	.760	.236	.570		.1332
Maumee River, Station Pond				.,		57-		. 00-
Rapids	2	.262	.423	.765	.233	.475	.164	.180
Eurynia recta, Compariso	N UPP	er Oh	10 DR.	AINAGI	E WITH	LAKE	ERIE.	
		1		T . C	11			-
Presque Isle, Lake Erie (98-124)		.284	.389	.783	.2169	000		.1239
Allegheny tributaries (22-34)		.263	.419	.783	.210	.518		.1592
Presque Isle, Lake Erie (98–124)		.28.4	.389	.783	.2169	000		.1239
Allegheny River (10–17)		.260	.325	.834	.1756	.526	.1328	.1507
Presque Isle, Lake Erie (98-124)	15	.284	.389	.783	.2169	.555	.1587	.1237
Ohio River (55–56)	15	.308	.436	.834	.1727	•593	.1976	.1846
Lampsilis luteo	la rosa	icea, L	ake E:	RIE DI	RAINAG	E.		
La Plaisance Bay, Monroe Co.,								
Mich	7	.393	.579	.731	.266	.515	.205	.1757
Cedar Point		.395	.58.4	.755	.2.18	.540	.219	.1160
Presque Isle Bay		.474	.603	.752	.245	.510	.233	.0001
Port Colborne, Ontario	3	.339	.619	.733	.266	.564	.207	.2082
or consonic, ontario	3	1339	.019	.155		.304	1201	

TABLE IV.—Continued.

	No. Spec.	$\frac{DSD}{L}$.	$\frac{DPD}{L}.$	$\frac{PD}{L}$.	$\frac{AD}{L}$.	$\frac{PHL}{L}$.	AHL L	$\frac{DVD}{TH}$.
Lake Erie, Port Dover Blanchard River, Hancock Co.,				-	-	.527		
Ohio	3	.334	.589	.752	.248	.489	.2078	.1236
Rapids	3	.391	•543	.755	.2.43	.519	.203	.1533
Maumee River, Roche de Boeuf Rapids, Beaver Creek, Williams Co., O.; Swan								
Creek, Lucas Co., O	7	.379	.607	.713	.289	.498	.221	.1277
Ten-Mile Creek, Toledo, O	4	.373	.575	.718	.275	.489	.2.46	.134

Lampsilis luteola rosacea, LAKE ERIE DRAINAGE.—Continued.

La Plaisance, Cedar Point (98-						1	
99)	17	.377	.585 .740	.273	.509	.2216	.1229
Presque Isle (101-120)	17	.419	.588 .738	.2987	.516	.2217	.1046
Presque Isle (101–120)	15	.388	.567 .741	.259	.515	.2231	.1034
Conneaut Lake (27-31)	15	.374	.585 .747	.255	.511	.208	.1235
Presque Isle (101–120)	17	.419	.588 .738	.2.487	.516	.2217	.1046
French Creek Drainage (22-34)	17	.375	.577 .737	1.263	.494	.2261	.1262
Presque Isle (101-120)	8	.386	.578 .7.44	.258	.521	.2219	.1171
Monongahela (45–46)	8	.444	.517 .756	.245	.548	.217	.163
Presque Isle, La Plaisance Bay							
(98-119)	28	.397	.587 .743	.263	.506	.2206	.1136
Beaver Drainage (60-85)	28	.373	.589 .726	.272	.504	.230.1	.1314
Presque Isle (101–120)	I 2	.431	.596 .754	.2.441	.516	.221	.1051
Allegheny River (12–17)	I 2	.315	.583 .731	.265	.516	.273	.1508

Lampsilis ovata Canadensis, LAKE ERIE DRAINAGE.

La Plaisance Bay Cedar Point Lake Erie, Vermilion Co Lake Erie, Port Dover Port Rowan, Canada	8 2 3	.387 .544 .489 .495 .498	.783 .730 .764	.713 .714 .715	.257 .284 .283	·434 ·453 ·473	.244 .266 .1710	.0867 .0810 .0754
Conneaut Creek, West Spring- field	2	.455	.721	.702	.300	.439	.215	.0918

Lampsilis ovata, COMPARISON UPPER OHIO DRAINAGE WITH LAKE ERIE.

Lake Erie (98–100)	I 2	.504	.763	.709	.290	.432	.23 .103	8
Presque Isle (101–119)	12	.485	.752	.685	.318	.444	.2104 .089	5
Allegheny tributaries (4, 22–34)	17	.463	.743	.693	.310	•459	.25 .086	8
Presque Isle (101–119)	17		.751	.677	.325	.437	.219 .089	5
Presque Isle (101–119)	23		.746	.680	.321	.434	.2202 .085	6
Allegheny River (7–17)	23	.456	.705	.699	.276	.420	.206 .101	I
Presque Isle (101–119)	I 2	.485	.752	.685	.318	+444	.2104 .089	5
Beaver Drainage (60-85)	12	.442	.648	.682	.316	439	.2321 .104	9
Presque Isle (79)	9		.761	.676	.328	.438	.198 .090	9
Beaver River (79)	9	.445	.705	.652	.3.48	.403	.2127 .066	5
Presque Isle (101–119)	5	.472	.758	.686	.316	.446	.1953 .091	8

4. Correspondingly, the posterior hinge-length (*PIIL*) tends to have a greater development in Lake Erie, and, as observed in the table, is apparently positively correlated with the posterior development of the shell. The converse appears to be established, *i.e.*, that the anterior hinge-length is best developed in the Upper Ohio, etc., and also positively correlated with the greater anterior development of the shell.

5. Thickness, as a rule, is greater outside of Lake Erie.

We have seen that the ancestors of the Lake Erie and Upper Ohio forms were derived from the same stock. Since some of the latter went over into the lake and became modified, the problem this investigation tries to answer is "How have they changed?" *The answer is given in the preceding paragraphs*. If we put a shell in the *lake environment* we may expect it will change its morphological features, not at random, but in a distinct, determinate, or orthogenetic direction, as is now seen by the fact that other shells behave the same way.

IX. CORRELATIONS.

From Tables IV and V also the following correlations may be derived in the case of shells from Lake Erie:

I. A decided tendency toward a greater degree of inflation (DSD) width, associated with less dorso-ventral diameter (DVD) height.

2. In all but two species (to which there are exceptions) there is a greater degree of inflation associated with greater posterior development of the shell (PD).

3. In all but two species greater posterior diameter is associated with greater posterior hinge-length.

4. Greater *DSD*, *PD*, *PHL*, and less *DVD* are associated with less thickness.

5. These dimensions correlate with one another throughout the lake environment.

With regard to the Upper Ohio shells the following seems true, viz.:

I. A decided tendency toward a less degree of inflation associated with a greater height and length of shell.

2. Less degree of inflation with a greater anterior development.

3. In most species, greater anterior development with greater length of anterior hinge-line.

4. Less *DSD*, greater *DVD*, *AD*, *AHL*, associated with greater thickness.

5. These dimensions correlate with one another throughout the environment.

Anticipating to a certain extent results obtained in another investigation, it may be said, that if, measurements from shells collected from all parts of the Ohio Valley (rather than those solely from the headwaters) be compared with those from Lake Erie, the Lake Erie shells are distinguished by their almost perfect correlation of dimensions as above, as distinguished from the negative aspects evinced by the polymorphic Upper Ohio forms, coming really, as I hope I have shown, from a variety of environments rather than a single fairly constant one. Uniformity in environment, therefore produces a uniformity of effect upon these species of Naiades in most cases.

X. Suggestions as to Causes of Facts.

It is thought well to again give a short summary of the physical and biological conditions present in Lake Erie and the Upper Ohio Drainage as they appear to be concerned with the *Naiades*.

LAKE ERIE.

Water colder than in Upper Ohio, but with more even regulation of temperature. Currents much less rapid than in streams; water less agitated, except by moderate currents as indicated; carrying but little sediment. Bottom composed of pebbles, sand, or mixture of these, depending on region of lake, with coarser sediment derived from wear of land. Temperature conditions favor a more uniform production of food, while the water contains more lime.

UPPER OHIO DRAINAGE.

Water warmer than Lake Erie, greater extremes of temperature. Streams more rapid than currents of Lake Erie and more greatly agitated; frequent falls and rapids; short stretches of quiet pools. Rivers carry a load of debris which moves quickly over bottom, consisting of mud, glacial till, cobbles. Food conditions (due to extreme of temperature), are less stable, even if at times more abundant.

REMARKS AND SUGGESTIONS CONCERNING RESULTS OBTAINED. (a) On Inflation of Shell.

Mr. Calvin Goodrich in a letter to the writer (1916), remarks that when colonies of shells are found in the lake, the members are sometimes moving about. Ordinarily, he states, it is not the usual thing for Unios to wander. This is indeed more frequently the case in spring when changing conditions impel migration, or at times when water becomes low in streams. We have seen that the *Naiades* of Lake Erie as a rule have a higher degree of inflation than those of the

Upper Ohio where the rapidity of the water is greater. It might seem that a shell having an exceptional degree of inflation would be at disadvantage in the short periods during which it might require to move about, for such would offer a greater surface to the water resulting in the impediment of its motions, let alone the obstruction the shell might encounter from a rocky bottom. In the lake, where there is little agitation of the water it might freely expand with less danger to itself. I feel there is something more than speculation about this hypothesis, inasmuch as certain other unpublished observations tend to show that even in rivers the greater degree of inflation is found where the current is less, as is also indicated in the resumé of the literature. As to the exception of A. ferussacianus, there is no clue whereby its exception to the law of inflation may be explained. Dr. Ortmann says: "It prefers small streams with sandy bottom and little current, frequently going into lakes." This statement of its favorite life conditions largely recalls Lake Erie. In the years of Dr. Ortmann's collecting (1909–18) he has obtained few or none of this species from the big rivers. Being somewhat primitive in character, it may well have reached in many respects the limit of adaptation compatible with biological balance, and the lake environment does not require the extreme of variation for it in this respect. This has some substantiation in the fact that the tabulation shows it to reach its greatest development in the Upper Ohio Drainage.

As to the length of the shell, my results corroborate those of the European investigators, who claim that it would be a useful adaptation, when connected with other characters, under the conditions of the environment in streams.

(b) On the Height of the Shell (DVD).

It was stated in the conclusion that there was a tendency observed for the shells as a whole to be higher in the Ohio. This may be a compensation in growth for the decreased inflation mentioned, or it might be more useful in getting about through the coarser gravel and mud, just as the shape of the more rapidly swimming fishes enables them to cut the water. At any rate this corresponds well with greater length. *Fusconaja*, *L. ovata*, and the majority of *Proptera* were higher in Lake Erie, together with even numbers of other shells. *Fusconaja* burrows deeply in fine gravel and sand, loves small streams and running water, disliking rough bottom and favors bars of fine,

firmly packed gravel. Many of its favorable conditions are found in Lake Erie as may be observed. Possibly its most enjoyable condition is found in a lucustrine environment, as indicated by the tabulation, which shows that of seven dimensions taken, five are greater there. Prophera is a lively shell, crawls about much, likes a steady current with rocks, gravel, and sand firmly packed. It would seem a greater height is more useful to it in moving about the rivers with their conditions than in Lake Erie. Here paucity of material compelled me to use that of the Ohio and I am uncertain as to the conclusions to be drawn, at least with regard to their stability. L. ovata ventricosa likes quiet pools and eddies, gravel partly covered with mud. Here again difficulty with material arises. L. ovata passes upstream into L. ovata ventricosa. To what extent this took place in my material, and what precisely the differences were, there was no way of telling, due to the puzzling intergrades. Mr. Goodrich states that in Lake Erie this mussel has a trick of burrowing completely below the surface and passes its gills fan-like from the shell, in which case the height of the shell might facilitate the burrowing process. However, other species do the same. Wilson and Clark (54) remark that this mussel becomes smaller towards the lakes, and perhaps we have here another evidence of compensatory growth. Specimens of L. ovata from "big rivers" are higher than those of the lakes.

(c) On the Comparative Size of the Anterior and Posterior Portions of the Shell.

It will be remembered that shells from the Upper Ohio were found to be better developed anteriorly and less posteriorly than those of Lake Erie. The need of sometimes having to move against opposite and unfavorable influences is met in the *Naiades* by the development of a foot, situated anteriorly. The physical nature of conditions in Lake Erie offer less impediment to such movements. Thus it may happen that the greater use of the foot in the Ohio would result in its greater enlargement, and have an ultimate effect in the development of the shell covering it. Such hypothesis could only be proven experimentally, inasmuch as other factors may be concerned. Sell found that the anterior part of the shell was best developed in rivers, and from the results of another investigation I may state that in the Monongahela, where conditions more closely resemble those of Lake